

Demographics and disturbance history of a boreal old-growth *Picea abies* forest

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Abstract

Question: To what extent do tree growth, mortality, and long-term disturbance patterns affect stand structure and composition of an old-growth *Picea abies* forest?

Location: Boreal Sweden.

Methods: We linked data from three 50 m × 50 m permanent plots established in 1986 with dendrochronology data to evaluate tree growth and mortality over an 18-year period and to describe a several-hundred-year disturbance history for this forest type.

Results: Averaged over all diameters, *P. abies* trees had an annual mortality rate of 0.60%; however, diameter had a striking effect on both growth and mortality, with trees of intermediate diameters (ca. 20–30 cm) showing faster growth and lower mortality. Their increased vigor gave rise to a diameter distribution resembling the ‘rotated sigmoid’ (not reverse-J) proposed for such conditions, and it led to a deficit of snags of intermediate diameters. Slow-growing trees had an increased likelihood of dying. Although recruitment occurred in most decades over the past 400 years, two prominent recruitment peaks occurred (mid 1700s and 1800s), neither of which appeared to cause a shift in tree species composition. The lack of fire evidence suggests that fire was not responsible for these recruitment peaks.

Conclusions: Taken together, these results depict a rather impasse system, where canopy trees die slowly over decades. Field observations suggest that fungal infections, mediated by wind, account for much of the mortality during these periods of relative quiescence. However, these periods are at times punctuated by moderate-severity disturbances that foster abundant recruitment.

Keywords: Dendrochronology; Late-successional forest; Mortality; Permanent plot; Rotated sigmoid diameter distribution; Wood-decay fungi; Woody debris.

Nomenclature: Mossberg & Stenberg (2003).

Abbreviation: DWD = Down woody debris.

Introduction

The boreal forest constitutes one of the largest biomes on earth, covering 11% of the earth’s terrestrial surface (Bonan & Shugart 1989). Although fire is generally considered the primary natural disturbance agent in boreal forests, sizeable areas can exhibit quite long fire-free periods. The research emphasis historically placed on stand-replacing fire has likely overshadowed the role of small-scale disturbances that occur in late successional boreal forests (McCarthy 2001). As a consequence, much remains unknown about basic autogenic processes, such as tree growth and mortality, as well as the role of non-catastrophic disturbances that occur under late-successional conditions.

For example, despite the commercial importance and wide geographical range of *Picea abies*, few studies have addressed basic demographics of late-successional forests dominated by this species. These studies are scarce in part because late-successional forests are now scarce in Fennoscandia, owing to 150+ years of intensive harvesting pressure. We know of only two studies (Hytteborn et al. 1991; Linder 1998) that report tree mortality rates under such conditions, the two showing quite different estimates. Although a number of studies have addressed disturbance dynamics in this forest type (e.g., Hofgaard 1993; Wallenius et al. 2005), the results have been variable and inconsistent, particularly regarding the role of fire and the cause of apparent cohort structures. This inconsistency suggests a level of complexity often not attributed to this forest type, and it demonstrates the need for additional study.

In late-successional forests governed by gap-phase processes, periodic canopy tree mortality effects changes in resource availability, species composition, and stand structure. Several tree attributes interact to determine risks of mortality. Of particular interest is the diameter

dependence of mortality, as it strongly influences forest stand dynamics and structure. The diameters at which trees die determine the size distribution of snags and down woody debris (DWD), as well as the size of canopy gaps, given that larger trees generally form larger gaps (Dahir & Lorimer 1996). The mode of death for individual trees, either catastrophic or slowly progressing, determines the rate of resource reorganization and hence the rate of response of neighboring vegetation (Kneeshaw & Bergeron 1998). Similarly, the temporal pattern of canopy mortality, whether stable or pulsed, strongly influences stand structure and composition (Fraver & White 2005), as well as the population dynamics of deadwood-dependent organisms (Jonsson et al. 2005).

Such information has direct applications to forest conservation and management. For example, understanding the population dynamics of the 600+ deadwood-dependent species currently red-listed in Sweden (Gårdenfors 2005) requires knowledge of tree mortality, and hence deadwood additions, under natural conditions. The lack of demographic and disturbance information has hampered modelling efforts of deadwood abundance, which currently rely on mortality derived from managed forests monitored over a recent ten-year period, and assume constant mortality through time (Ranius et al. 2003). Further, developing silvicultural systems meant to emulate natural disturbance (Seymour & Hunter 1999), requires an adequate understanding of historical disturbance frequency, extent, and severity, including the range of variability. This is particularly important in the boreal regions, where ecological forestry has for the most part adopted large-scale, stand-replacing fire as the model to emulate. Much less consideration has been given to emulating natural disturbances of late-successional boreal forests, despite the recognition of boreal regions with quite long (thousands of years) fire-free periods (e.g., Cyr et al. 2005; Wallenius et al. 2005).

In the present study, we investigate tree demographics and long-term disturbance histories of late-successional *P. abies* forests in boreal Sweden. Our study is based on a re-inventory of permanent plots, with individually tagged and mapped saplings and trees, established in 1986. We augment these data with dendrochronological analyses on these same plots to extend the temporal reach of the investigation. Our specific objectives were (1) determine the background tree mortality rates; (2) evaluate the extent to which tree size influences growth and mortality rates; (3) assess the influence of these demographics, as well as past disturbances, on current forest composition and structure. The results provide baseline data to aid the conservation and management of late-successional boreal spruce forests.

Methods

Study area

The study was conducted in the Gardfjället Nature Reserve of Västerbotten County, boreal Sweden (centered at 65°26' N, 15°53' E). The closest weather station (Dikanäs) lies ca. 10 km southeast of the Reserve. Mean annual precipitation is 667 mm; mean monthly temperatures range from -11.6 °C in January to 12.3 °C in July, with an annual mean of 0.4 °C (Swedish Meteorological and Hydrological Institute, records 1945-2005). The substrate includes a thick (to 15 cm) layer of humus underlain by fine-grained mineral soil derived from glacial till. Field observations confirm the absence of logging within the Reserve.

Forests in the Reserve are clearly dominated by *P. abies*, although *Betula pubescens* may constitute as much as 10% of the basal area. *Salix caprea* and *Sorbus aucuparia* are present in low abundance. The field layer is dominated by *Vaccinium myrtillus*, with *Gymnocarpium dryopteris*, *Cicerbita alpina*, *Maianthemum bifolium*, *Geranium sylvaticum*, and other herbaceous plants occurring in patches. Tree density is rather sparse, and trees generally do not form closed-canopy stands. *P. abies* is quite tolerant of shade, and seedlings and saplings can persist in the shaded understory for extended periods; *B. pubescens* is generally considered intolerant of shade.

Field and laboratory procedures

The three plots used in this study were established in 1985-1986 by the fourth author as controls against which the effects of clearcutting could be assessed (Esseen 1994; Jönsson et al. 2007). Plots were 50 m × 50 m, situated ca. 550 m a.s.l., with the distances between them ranging from 0.5 to 3.2 km. During the initial inventory, species, diameter at breast height (DBH, 1.3 m), and height were recorded for all living trees and snags ≥ 5 cm DBH. Saplings of *P. abies* (stems ≥ 1.3 m tall and < 5 cm DBH) were similarly inventoried. We inventoried these plots again during the summer and fall 2004, recording diameter and mortality, when found, for all previously inventoried individuals.

We inventoried all down woody debris (DWD) to better assess the mortality that had occurred prior to the initial inventory and to augment the structural description for the late-successional stage of this forest type. For each DWD piece originating inside the plot, we recorded length, diameter at each end, direction of fall (azimuth), decay class (following the eight-class system of McCullough 1948), and species (when not precluded by advanced decay). Only pieces with a diameter at the largest end greater than 10 cm were inventoried. We

noted if pieces had been uprooted or snapped (marked fracture with splintering), as these provide strong evidence of wind storms (Worrall et al. 2005); we refer to these as windthrows. In contrast, DWD not wind snapped often showed blunted breaks, suggesting they had been weakened by fungi before falling; we refer to these as deadfalls. The volume of each DWD piece was calculated as a conic-paraboloid (Fraver et al. 2007); tree and snag volumes were calculated from height and DBH following formulae in Näslund (1940).

We extracted one increment core at breast height from each tree ≥ 10 cm DBH to determine growth patterns and age structures. We made no attempt to estimate actual tree ages (i.e., years since germination) because (1) even cores extracted from lower stems and root collars yield substantial underestimates of actual ages (Niklasson 2002); and (2) shade tolerant species such as *P. abies* do not depend on open conditions for establishment, meaning their ages since germination may be poorly linked to previous disturbances (Lorimer 1985), an emphasis of this study. We thus express the number of annual rings at breast height as the recruitment age. Because the work was conducted in a strict reserve, we were unable to extract radial cross-sections for dating snags and DWD. Instead, we extracted large diameter (12 mm) increment cores for this purpose in an attempt to reduce the visual impact of deadwood sampling. All increment cores were mounted and sanded to a fine polish using standard methods. Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted following the marker-year method of Yamaguchi (1991), with verification by COFECHA (Holmes 1983).

Analysis of tree demographics

To reduce the bias introduced by using radial growth when comparing stems of various diameters (e.g., radial growth of 1.0 mm per year translates to quite different stem wood growth on trees 10 cm DBH and 60 cm DBH), we used basal-area increment (cm^2) over the 18-yr sampling period to characterize tree growth. When compared to radial growth, basal area growth may provide a more robust assessment of wood production and tree vigor (LeBlanc 1993). It was calculated for each tree from measured ring widths, correcting for off-center piths using methods and rationale presented in Frelich (2002). By convention, we included bark in the calculation, which required estimations of bark thickness in 1986 and 2003. For *P. abies* we used our in-house equation: $\text{SBT} = 0.01852 + 0.0341 \times \text{DIB}$, where SBT is single bark thickness and DIB is diameter inside bark, both in cm. This equation is based on 123 samples ranging in diameter from 2 to 52 cm. For trees from which an intact

core could not be extracted (8% of trees), basal-area growth was estimated from field measured diameters in 1986 and 2004. Because growth was calculated from tree-ring data, growth analyses were conducted only on trees ≥ 10 cm DBH in 2004. Small sample sizes for *B. pubescens* precluded analyses of growth and mortality by diameter class. In no case did we test for differences between plots. Our scale of inference was the spruce forest within the Reserve; plots simply represent a range of conditions encountered there.

Due to unequal variance among diameter classes, we used a Kruskal-Wallis test to determine if growth (basal area accrued) of *P. abies* differed by diameter class, based on the following six classes (midpoints, cm): 12.5, 17.5, 22.5, 27.5, 32.5, and >35 . Mortality was calculated as the number of individuals that died during the sampling period (1986–2004) expressed as a percent of those alive in 1986. The annual mortality rate is this figure divided by 18 years. We tested if the mortality rates of *P. abies* differed by diameter class using contingency-table analysis (based on raw numbers of living and dead in each class). Using data pooled across diameter classes, we tested if the annual mortality rate of *B. pubescens* differed from that of *P. abies*, again by contingency-table analysis. We tested by logistic regression whether recent growth rates of *P. abies* trees influenced the likelihood of dying.

Analysis of long-term forest dynamics

In forests dominated by shade tolerant species forming closed canopies, growth releases evident on surviving trees provide valuable information on past disturbances (Lorimer 1985). However, given the canopy sparseness in this system, the growth-release method has quite limited use. A preliminary evaluation of the method revealed that it recorded only a subset of the windthrow events known from the permanent-plot data, and none of the slow deaths of snags. For this reason, the dendrochronological methods were limited to analyses of recent growth rates, estimation of the mortality year for deadwood cores (determined by crossdating), and determination of recruitment ages. Data from dated deadwood was included in the age distributions in order to bolster information on recruitment during the earliest decades. To obtain a cursory assessment of past wildfires, we searched each plot and surrounding areas for charred deadwood and fire scars on living or dead trees. We also dug five soil pits (to ca. 30 cm depth) in the vicinity of each plot and sifted organic and mineral soil searching for macroscopic charcoal (particles greater than 1 mm). To assess the role of wind as a disturbance agent, we analyzed the fall directions of all downed trees (windthrows and deadfalls analyzed separately) by Rayleigh's test for circular uniformity (Batschelet 1981).

Results

Forest composition and structure

P. abies clearly dominated these stands (94% of basal area), with *B. pubescens* (6%), *Sorbus aucuparia* (<1%), and *Salix caprea* (<1%) as associated species. Data from all plots pooled reveal a mean living-tree basal area of 30.3 m².ha⁻¹, density of 609 trees/ha, and volume of 192.7 m³.ha⁻¹. Snags had a mean basal area of 3.0 m².ha⁻¹, density of 51 snags/ha, and volume of 16.3 m³.ha⁻¹. The average annual snag addition rate was 0.7 m³.ha⁻¹, or 1.9 stems/ha. The mean volume of DWD was 76.8 m³.ha⁻¹, of which *P. abies* comprised 96% and *B. pubescens* the remainder (excluding pieces that could not be identified). The average annual DWD addition rate was 1.0 m³.ha⁻¹, or 1.8 pieces/ha. Structural characteristics of each plot are shown in Table 1.

Tree demographics

P. abies had significantly lower mortality in intermediate diameter classes (Fig. 1; $\chi^2 = 26.0$, $df = 7$, $p = 0.0005$). This appeared to be true for *B. pubescens* as well, although small sample sizes precluded analyses. Using data pooled across diameter classes, the annual mortality of *B. pubescens* exceeded that of *P. abies* ($\chi^2 = 8.60$, $df = 1$, $p = 0.003$), with the overall mean annual rates for *B. pubescens* (1.24%) nearly double that of *P. abies* (0.64%). For trees ≥ 10 cm DBH, these values were 1.15% and 0.60%, respectively. *P. abies* trees with lower growth rates had an increased likelihood of dying during the sampling interval (logistic regression likelihood ratio $\chi^2 = 7.12$, $p < 0.008$). In fact, roughly 80% of all dated dead *P. abies* ($n=47$) showed either persistent slow growth or steadily declining slow growth in the decades preceding their deaths (Fig. 2). *P. abies* growth rates were highest in intermediate diameter classes (Fig. 1), with the difference being highly significant (Kruskal-Wallis, $\chi^2 = 63.3$, $p < 0.0001$). Windthrown trees represented only 14% of the mortality during the sampling interval; the remaining dead trees were deadfalls (44%) or snags (42%). Diameter distributions of living and dead *P. abies* trees are shown in Fig. 1.

Long-term forest dynamics

The recruitment age structure, which includes dated deadwood, could best be described as multi-aged with recruitment pulses (Fig. 3). Recruitment occurred in most decades over the past 400 years, albeit in quite low numbers in several decades. The pulse beginning ca. 1745, notable on all three plots, persists for three to four decades. *B. pubescens* shows rather continuous recruitment over the past 160 years, although in low abundance relative to *P. abies*. The maximum longevity of *P. abies* (recruitment age of 379 yrs) greatly exceeded that of *B. pubescens* (163 yrs).

We found neither charred deadwood nor fire-scarred trees in the study area. Soil sampling revealed no macroscopic charcoal fragments in any of the 15 pits. Analyses of fall directions for windthrows showed a significant uniform orientation (mean azimuth of 80°, Reliegh's $p < 0.001$, $n = 17$, circular SD = 21.8°). Directions for deadfalls also showed uniformity, although with much higher standard deviation (mean azimuth of 100.6°, Reliegh's $p < 0.001$, $n = 81$, SD = 52.1°). These easterly fall orientations reflect storm winds predominantly from the west: winds of gale force or greater (17.2 m. s⁻¹) had a mean azimuth of 269° ($p < 0.001$, $n = 54$, circular SD = 26.9°, records pooled from four local meteorological stations between 1961 to 2000; Swedish Meteorological and Hydrological Institute 2005).

Discussion

Forest composition and structure

The stands clearly exhibit characteristics of old-growth forests: abundant snags and DWD in various states of decay, a range of tree ages and sizes, dominance by a shade-tolerant tree species, and diverse canopy structures. The structural attributes shown in Table 1 generally fall within the ranges reported from boreal Fennoscandia (Siitonen 2001). To the best of our knowledge, our annual snag and DWD addition rates (0.7 m³.ha⁻¹ and 1.0 m³.ha⁻¹, respectively, over the 18-year sampling period) are the first reported under natural conditions for this forest type.

Table 1. Basal area (BA, m²), number of stems, and volume (vol., m³), including down woody debris (DWD), for the three old-growth *P. abies* plots. Trees and snags refer to stems > 10 cm DBH.

Plot	Live Trees (value.ha ⁻¹)			BA	Snags (value.ha ⁻¹)		DWD Vol.ha ⁻¹
	BA	Stems	Vol.		Stems	Vol.	
A	34.4	612	224.5	3.6	48	20.0	80.2
B	28.9	664	180.3	3.0	64	16.2	67.8
C	27.7	552	173.5	2.4	40	12.6	82.4

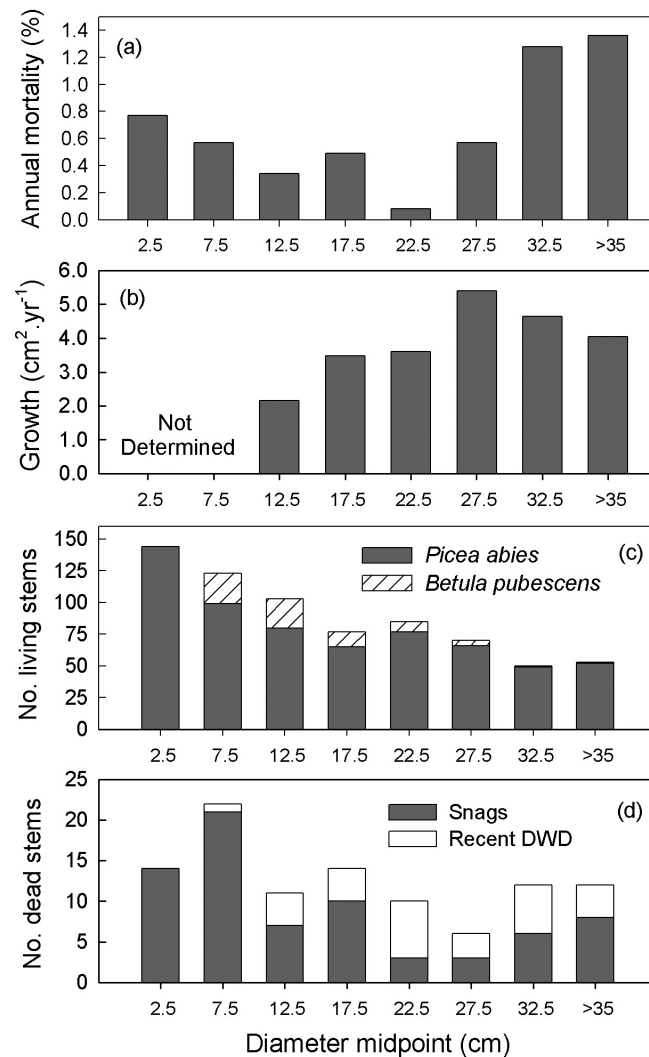


Fig. 1. **a.** Annual mortality of *P. abies* by diameter class showing lowest mortality in intermediate diameters. **b.** Median annual basal area growth of *P. abies* by diameter class showing most rapid growth at intermediate diameters. **c.** Diameter distribution for living trees, suggesting a rotated sigmoid form. **d.** Diameter distribution for *P. abies* dead wood (snags plus intact DWD) showing a slight deficit in the intermediate diameters.

Tree demographics

P. abies (trees ≥ 10 cm) had an annual mortality rate of 0.60% over the 18-year sampling period. We know of only two previous studies of mortality for this species under old-growth conditions. From a mixed-species stand in mid-boreal Sweden, Linder (1998) found an annual mortality rate of 0.45% (calculated from his Table 3); from a *P. abies* stand in southern boreal Sweden, Hyttenborn et al. (1991) reported an annual mortality rate of 1.12%. In the present study, the mortality rate for *B. pubescens* trees (1.15%) was nearly twice that of *P. abies*. This difference reflects the expected longevity of the two species: the maximum recruitment age for

P. abies was 379 years and for *B. pubescens* 163 years. Similarly, Woods (2000) found higher mortality for *Betula alleghaniensis* when compared to the co-occurring long-lived conifer *Tsuga canadensis* in northern Michigan. Ages obtained from dead trees, however, provide a better estimate of typical longevity (Lorimer et al. 2001). The mean recruitment age at time of death for *P. abies* was 178 years, which corresponds quite well with the estimated turnover time of 167 years (i.e., the time it would take for mortality to 'turn over' the stand, calculated as inverse of annual mortality). We note that the actual age (since germination) of *P. abies* may be considerably greater than the recruitment age, given that individuals can sustain decades of suppression in the

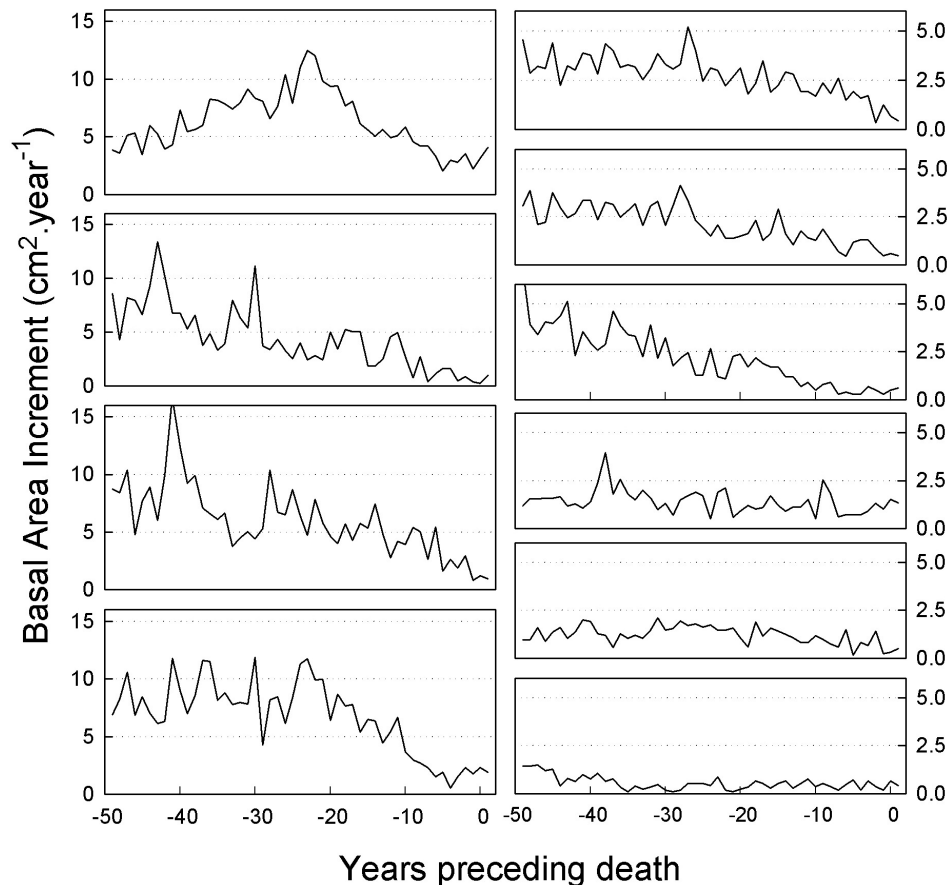


Fig. 2. Selected *P. abies* tree-ring series showing steadily declining or persistently slow basal area growth in the decades preceding tree death. Over 80% of dated dead trees showed similar growth patterns, suggesting senescence as the primary mode of death. Note that vertical axes are on different scales.

seedling stage before reaching breast height.

P. abies had the lowest mortality rates in intermediate diameter classes, resulting in a U-shaped pattern across diameter classes (Fig. 1). This differential mortality is reflected in turn in the size structure of snags, where the intermediate diameters are underrepresented; it is less obvious for intact DWD (pieces where former DBH could be estimated) (Fig. 1). This U-shaped mortality pattern has been reported in other old-growth forests (e.g., Lorimer et al. 2001) and suggests that different mortality agents predominate in various developmental stages of individual stems. The relatively high mortality in saplings and small trees is consistent with the well known risk owing to competition (Kozłowski et al. 1991). The increased mortality seen in large trees may result from increased maintenance respiration and decreased hydraulic conductivity, both of which can lead to an unfavorable balance between photosynthesis and respiration (Ryan et al. 1997). Larger and older trees are also more likely to be infected by fungi (Rouvinen et al. 2002). Although windthrow is a greater risk for larger conifers

(Canham et al. 2001), our results suggest that it plays a lesser role than other mortality agents: it accounted for only 14% of the observed mortality.

Our results showed that *P. abies* trees with lower growth rates had an increased likelihood of dying. Similarly, Bigler et al. (2004) and Das et al. (2007) found that consistently slow or declining growth were reliable indicators of impending tree death for various conifer species. Our finding of higher growth rates in intermediate diameter classes (Fig. 1) provides a corollary to the U-shaped pattern of mortality, assuming faster growth to be a measure of tree vigor. Taken together, the diameter-related trends seen for mortality and growth simply suggest that trees of intermediate diameters represent an optimal stage that follows escape from intense competition yet precedes size-related risks to mortality. Importantly, they support the contention by Goff & West (1975) that rapid growth (although these authors imply diameter, not basal-area, growth) and low mortality for intermediate diameters could explain the failure of many old-growth stands to fit the often-cited reverse-J diameter

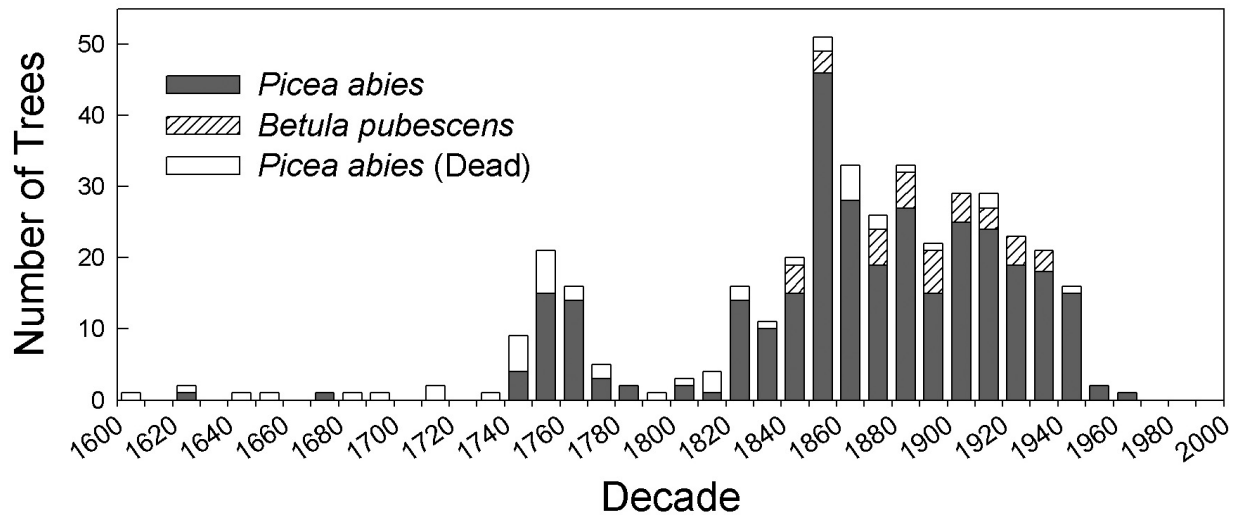


Fig. 3. Recruitment age-class distributions showing a multi-aged structure with two distinct pulses, suggesting moderate severity disturbances in the mid-1700s and mid-1800s. The inclusion of dated deadwood adds important recruitment information, particularly in the early decades.

distribution. Goff & West (1975) proposed that at the stand scale this combination of traits would produce a 'rotated sigmoid' form (log abundance vs. diameter), which has been supported by simulation modeling (Lorimer & Frelich 1984) as well as empirical studies (Lorimer et al. 2001; Westphal et al. 2006). This issue has recently gained renewed interest because of its direct application to forest sustainability (Rubin et al. 2006), reasoning that the diameter distribution found under natural conditions may provide the targeted post-harvest distribution for sustainable multi-aged silvicultural systems. The diameter distribution found here resembles the rotated sigmoid (Fig. 1); however, the marked temporal pulses in recruitment (Fig. 3) confound the interpretation of any of the theoretical distributions, which assume equilibrium with regard to recruitment and disturbance.

Long-term disturbance history

Although age structures provide a rather crude proxy for previous disturbance (Johnson et al. 1994; see Methods), the pronounced peaks in tree recruitment (Fig. 3) do suggest a moderate-severity disturbance ca. 1850 and a disturbance of at least moderate severity ca. 1750. Fire is typically implicated as the primary natural disturbance agent in this region; however, the lack of evidence (fire scars, charred deadwood, macroscopic soil charcoal) suggests that fire was not responsible for these disturbances. We note that our soil-pit method may not entirely rule out past fires; a proper assessment of long-term fire history would require more detailed paleoecological work (e.g., Cyr et al. 2005). However, when taken together with other evidence it does call into question the prevalence of fire as

a disturbance agent in this Reserve. Similarly, numerous case studies from the boreal zone have reported areas with quite long fire-free periods (e.g., Steijlen & Zachrisson 1987; Hofgaard 1993; Kuuluvainen et al. 1998; Wallenius et al. 2005; Cyr et al. 2005). Though fire indisputably plays an important role in boreal forests, several authors have suggested that the role of stand-replacing fire has been overestimated in parts of the northern boreal zone (Bergeron et al. 1998; McCarthy 2001).

Several workers in Fennoscandia have implicated decadal-scale climatic fluctuations to explain pulses or hiatuses in *P. abies* recruitment (Kullman 1986; Steijlen & Zackrisson 1987; Hofgaard 1993). However, if climate were the driving force, such pulses would likely be expressed regionally. Neither of the pulses in the present study coincides with those of the above mentioned studies, nor is there strong agreement among those studies. Further, pulses in recruitment cannot be attributed to masting, by reason of its semi-annual, not decadal, fluctuation (Selås et al. 2002), as well as the regional lack of synchrony.

We suspect the recruitment pulses are the result of wind storms. Unfortunately, direct evidence for long-removed storms is lacking, as deadwood resulting from these events has decayed. However, winds of gale force or greater are not uncommon (above) in this region in modern times, where they are known to cause moderate-severity damage (Esseen 1994).

We might expect these disturbance pulses to have a marked influence on tree species composition. Surprisingly, however, nothing in our results points to a successional shift in tree composition. Had *Pinus sylvestris* colonized following either disturbance pulse, or had *B.*

pubescens (shorter lived) colonized *en masse* following the ca. 1850 pulse, evidence would still be visible in the living and dead tree components. Yet *P. sylvestris* (living or dead) is currently absent, living *B. pubescens* is present only in low abundance, and deadwood species composition closely resembles that of the living tree composition. Similarly, Hofgaard (1993) found that natural disturbance in boreal Sweden simply perpetuated *P. abies*, and comparable findings have been reported from North American spruce forests (Fraver & White 2005). The loss of canopy trees would promote advance regeneration of *P. abies* (seedlings and saplings established prior to disturbance) toward the canopy; both *P. abies* and *B. pubescens* would regenerate by seed on exposed mineral soils of uprooting mounds (Kuuluvainen 1994); and several decades later, as fallen logs become suitable substrate (Arnborg 1942), additional *P. abies* regeneration would take place on these nurse logs (Hofgaard 1993, pers. obs.). This sequence of events may explain the protracted recruitment peaks for *P. abies*, for example, beginning ca. 1745 and spanning several decades (Fig. 3).

But what background mortality processes occur between moderate-severity disturbances? Evidence from field observations, growth trends, and fall direction of deadfalls suggests that fungi play a significant role, with wind as a contributory factor. First, working in this same Reserve, members of our laboratory found that 70% of recently fallen *P. abies* logs were infected by heart-rot fungi such as *Phellinus chrysoloma* and *Stereum sanguinolentum* (Edman et al. 2007). Both species are regionally common; they infect living, often injured or poor vigor, *P. abies*. Non-lethal top breaks caused by heavy snow loads, which were seen on 12% of the trees in this study, no doubt serve as infection courts for wood-decay fungi, thus elevating their importance as mortality agents (Hennon & McClellan 2003). Second, our finding that roughly 80% of dead *P. abies* had either persistent slow growth or steadily declining slow growth in the decades preceding their death (Fig. 2) may point to fungi as a contributing factor. Cherubini et al. (2002) found similar fungal-induced declining growth prior to tree death in *Pinus mugo*. Third, blunted breaks seen at the base of many large deadfalls, coupled with their uniform fall directions (opposite that of regional storm-tracks), suggests that these trees had been basally weakened by fungi prior to being toppled by wind (Worrall et al. 2005).

As in any case study, it is not clear if these findings can be generalized for *P. abies* forests throughout the region. They do, however, document processes and conditions within the range of natural variability encountered for this forest type, and they corroborate a number of other studies regarding forest structure, long fire-free periods, and multi-cohort age structures. Taken together, our find-

ings depict a rather impassive system, where canopy trees die slowly over decades, apparently owing to the combined effects of fungal infection and wind. However, at periodic intervals moderate-severity disturbances, likely windstorms, remove a substantial portion of the canopy, thereby releasing advance regeneration and allowing the establishment of new individuals over protracted periods. Despite these disturbance pulses, nothing in our results points to a successional shift in tree composition following disturbance: canopy trees appear to be replaced by recruitment of the same species.

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